



TRACHEATION OF WINGS OF EARLY LARVAL INSTARS OF GOMPHUS.—SCHMIEDER.

The Tracheation of the Wings of Early Larval Instars of Odonata Anisoptera, with Special Reference to the Development of the Radius.

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In the wings of *Gomphus*, stages of tracheal development were found which corresponded to those found in *Anax*. The observations and remarks made concerning the wings of *Anax*, as regards their size at the various stages of tracheal development, the variability in the number of tracheae and tracheal branches, and the condition of the tracheae, whether simple or fascicled, apply also in a large measure to the wings of *Gomphus*, as is shown in figs. 9-14. (Figs. 9-13 are of *G. villosipes*, fig. 14 is of *G. exilis*.)

In addition it should be noted that, especially in the earliest stages, the wings of *Gomphus* show even greater variations than have been described for *Anax*. Fig. 9 is a wing 0.12 mm. in length from a larva 8 mm. long. It has only five tracheae, the anal being entirely absent. The radius is branched from its point of origin, the posterior branch is bent at right angles and its distal portion passes caudad and crosses over the four anterior branches of the media. It is often found that in early stages tracheae may be very elongated so that their distal portions pass either cephalad or caudad along the edge of the wing, and this fact, together with the observation that the courses of the tracheae are at this time indefinite and largely a matter of chance, indicates that the condition of the posterior branch of *R* in this wing has no relation to the crossing of a radial branch over *M1* and *M2*, which is found in later instars.

In fig. 10, a wing 0.15 mm. long from a 7 mm. larva, conditions are very different from the preceding, there being no less than eleven distinct tracheae originating from the transverse basal trunk. In this wing *R* is unbranched, and *M* has but two branches.

Figs. 11 and 12 are of the front and hind wings respectively of a 10 mm. larva. These wings are 0.23 mm. in length and again show noteworthy variations.

Figs. 9-12 then, represent the ontogenetic stages in *Gomphus* corresponding to the stages in *Anax* of figs. 1-3. The succeeding stage is shown in figs. 13 and 14,—wings which are 0.4 and 0.45 mm. long, and corresponds to that of figs. 4-7 of *Anax*. The differences in the sub-costa of figs. 13 and 14 are interesting, as is also the presence of an additional trachea between *R* and *M* in figs. 11 and 14, since such was never observed in *Anax*.

Can we derive from the foregoing observations any clew as to the identity of the vein *Rs*; can we now determine whether the trachea crossing *M1* and *M2* really represents *Rs* and that we should therefore call the vein which forms along its course and in the adult lies posterior to *M2* the radial sector?

Needham has shown that in many insects the veins of the adult may be formed independently of the tracheae and that a vein is not always supplied by its corresponding trachea. Indeed in the wings we are now considering, we see that the costa receives its tracheal supply in great part from the subcosta and radius. There is, therefore, no *a priori* reason for assuming that the trachea called *Rs* may not, although it is a branch of *R*, be supplying a vein which is a true branch of the media, especially since Tillyard has shown that in *Uroptala* the vein *Rs* is supplied by a branch of *M* as well as by a branch of *R*.

Referring again to our figures we note that the radius in the very earliest instars (figs. 2, 3, 9, 11, 12) usually shows two branches and that in the next instar it most often has two groups of branches (figs. 4, 5, 13, 14) representing the same two branches; and in addition to these a fine tracheal branch which passes backward and crosses over the two anterior branches of the media. The differences between *R* in figs. 4 and 5 and the same trachea in figs. 6 and 7 are easily explained by referring back to the conditions found in the preceding instar. All of the principal tracheae in this first stage are simple, they are not composed of fascicles of fine branches as in the two later instars. In passing from this instar to the next, the two branches of *R* seen in figs. 2 and 3 develop branches equaling themselves in caliber and pursuing a course more or

less parallel to the tracheae from which they have originated, thus producing the conditions shown in figs. 4 and 5. In fig. 4 the anterior of these two branches is now composed of three fine tracheae, the posterior branch is still a single trachea; in fig. 5 the anterior branch is three-branched, the posterior two-branched. In addition there is another fine branch, the trachea *Rs* of Needham. This trachea is always but a single fine strand in this instar and crosses over *M1* and *M2*. It can be interpreted only as a new outgrowth of the radius, appearing for the first time in this instar, and not as the original posterior branch of this trachea which has shifted its position. In fig. 1 the radius has no branches; a larva in which such a condition obtains would in the succeeding instar show a condition such as is represented in figs. 6 and 7. The distal end of the vein has produced a branch so that it is now double at the end, in the same manner as the two branches of *R* in figs. 2 and 3 have given rise to the two anterior groups of branches seen in fig. 5. In addition, *R*, in figs. 6 and 7, shows a caudal branch *Rs* which again is a new outgrowth, appearing for the first time in this instar, just as the small branches which have appeared on the anterior side of both *Sc* and *R* are new outgrowths. With respect to *M*, a similar observation might be made on the phenomenon of tracheal branching and on the presence of fascicles of tracheae where only single tracheae existed in the preceding instar. In fig. 8 is shown the instar following upon that which is represented in figs. 4-7. The fascicled condition is more evident than in the preceding instar and it is noted that *Rs*, which was heretofore always simple, has now also produced branches and is composed of a group or fascicle of three tracheae.

In the wings of *Gomphus* the same conditions obtain. The usual two-branched condition of the radius of the earliest stage is seen in figs. 9, 11, 12; and in figs. 13, 14, the next stage, in which the two radial branches have been replaced by two fascicled branches and in which there is an additional fine branch crossing over *M1* and *M2*.

It is evident then, that when a trachea or tracheal branch

appears it is at first a single strand and not until the following instar does it acquire a fascicled condition as the result of the formation of parallel branches. Therefore, I believe that the branch R_s , which appears in the instar shown in figs. 4-7 of *Anax*, and in figs. 13 and 14 of *Gomphus*, is a new tracheal outgrowth appearing first in this instar and that it is not the posterior branch of the two-branched radius of the preceding instar (figs. 2, 3, 9, 11, 12). This posterior branch of R (called R_s by Needham) really develops into R_1 , while the original R_1 of this first stage does not develop into any principal trachea, but the small branches of which it is composed pass forward into the region of the costal vein.

I believe the evidence I have given is sufficient to demonstrate that if the trachea which Needham refers to as R_s in his fig. 1, A, is the true R_s , then in the grown larva the trachea R_1 is really R_s , and the R_1 of Needham's figure is represented in later stages only by the fine tracheae which pass forward and supply the costa, or possibly it has become combined with R_s and the fine tracheae going to the costal vein represent branches of R_1 .

I have also shown that the tracheal branch of R which crosses M_1 and M_2 is not the original posterior branch of this vein which is seen in the first stage and which, according to Needham, has undergone a shifting in position, but rather that it is a new outgrowth of the radius and that in the instar in which it first appears it is already in the position which it occupies in the full grown larva. This trachea therefore, cannot be considered as representing R_s in the sense that it has developed by a shifting of the posterior branch of R which is observed in the earliest stage and which Needham has said must be R_s .

This study of the tracheation of the wings of two Anisopteros larvae has thus yielded not the slightest evidence that the trachea R_s of the earliest instar has undergone a shifting in position and has come to lie posterior to M_2 ; but rather it has shown that this trachea retains its original position and forms, at least in part, the R_1 of the grown larva. It has revealed that

the tracheal branch of *R* which supplies a part of the course of the imaginal vein *Rs*, appears as a secondary outgrowth whose purpose is to function as a part of the tracheal supply of a vein which for some reason has failed to receive a tracheal supply from the one of which it is properly a branch, the media. Unless we interpret *Rs* as a supplementary vein not homologous to any primitive one, we must accept the theory of Tillyard and consider it as a true branch of the media. As to the fate of the original *Rs*, the ontogenetic stages in the larva seem to indicate that, at least the tracheae corresponding to this vein, remain along the course of *R1*, and that possibly the vein *Rs* has combined with *R1* or has taken its place. This is the conclusion we should arrive at if we trusted in the ontogenetic stages to obtain a true account of phylogeny. However, I believe that our faith in such evidence should not be too implicit and that conclusions derived therefrom should not be accepted unless supported by other evidence which may develop out of a paleontological study.

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EXPLANATION OF PLATE XI.

- Figs. 9-13, Wing rudiments from larvae of *Gomphus villosipes*.
Fig. 9, Length of larva 8 mm., length of wing 0.12 mm.
Fig. 10, Length of larva 7 mm., length of wing 0.15 mm.
Figs. 11-12, Length of larva, 10 mm., length of wings 0.23 mm.
Fig. 13, Length of larva 12 mm., length of wing 0.4 mm.
Fig. 14, Wing rudiment from larva of *Gomphus exilis*; length of larva 10 mm., length of wing 0.45 mm.